On the singing habits of forest honeyguides of the Guineo-Congolian region, with a request for further information

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Sur le comportement vocal des Indicateurs forestiers de la région guinéo-congolaise, avec une demande pour plus d'informations. Des études en Afrique australe ont montré que les indicateurs chantent à des postes fixes occupés pendant des années. Le comportement vocal des espèces forestières de la région guinéo-congolaise reste mal connu, mais des observations opportunistes obtenues sur une douzaine d'années ont mis en évidence plusieurs traits particuliers: chez les indicateurs qui chantent perchés (genres *Indicator* et *Melignomon*), il y a séparation verticale des espèces; c'est l'Indicateur tacheté *Indicator maculatus* qui chante le plus bas (dans le sous-bois) et l'Indicateur de Willcocks *I. willcocksi* le plus haut (dans la voûte des émergents, avec une préférence pour *Piptadeniastrum africanum*). Les différentes espèces ont des horaires spécifiques de chant: l'Indicateur tacheté est le plus précoce (commençant une heure ou moins après l'aube) et l'Indicateur d'Eisentraut *Melignomon eisentrauti* le plus tardif (commençant environ sept heures après l'aube). Les indicateurs chantent plusieurs heures par jour à un poste fixe, mais la durée peut varier selon les espèces et semble particulièrement courte chez l'Indicateur d'Eisentraut (environ deux heures). Certaines espèces s'arrêtent de chanter 2–3 mois par an (Petit Indicateur *Indicator minor*, Indicateur de Willcocks) ou par périodes de plusieurs semaines (Indicateur à queue-en-lyre *Melichneutes robustus*, qui parade surtout pendant la longue saison sèche). L'Indicateur tacheté chanterait toute l'année; on manque d'informations pour les autres espèces.

La fidélité au site de chant d'une année sur l'autre a été démontrée pour plusieurs espèces (Petit Indicateur, Indicateur de Willcocks, Indicateur tacheté, Indicateur de Zenker *Melignomon zenkeri*). Chez une même espèce des genres *Indicator* et *Melignomon*, les sites réguliers de chant semblent assez dispersés (éloignés d'un kilomètre ou plus). Chez l'Indicateur à queue-en-lyre par contre, il existerait peut-être un système de lek, avec plusieurs individus participant à des parades aériennes dans une zone restreinte. Le bruit particulier produit par cette espèce proviendrait des mouvements des ailes et pas seulement de la queue. On ne sait presque rien du comportement de l'Indicateur pygmée *Prodotiscus insignis* (?parade aérienne), ni des habitudes de chant de l'Indicateur minule *Indicator exilis*. L'Indicateur de Zenker aurait un comportement vocal proche de celui de son congénère l'Indicateur d'Eisentraut (notamment par un horaire de chant en début d'après-midi), mais on a besoin de plus amples informations pour compléter le tableau chez cette espèce et d'autres.

Summary. Studies in southern Africa have shown that honeyguides sing at regular sites over many years. The vocal behaviour of forest species of the Guineo-Congolian region remains poorly known, but opportunistic observations over a dozen years have revealed some interesting features: among *Indicator* and *Melignomon* species (which sing perched), there is vertical separation between species, from Spotted Honeyguide *Indicator maculatus* singing low down (in the understorey) to Willcocks's *I. willcocksi* high in emergents (with special preference for *Piptadeniastrum africanum*). Each species has a particular timetable for singing, the earliest being Spotted Honeyguide (starting an hour or less after dawn) and the latest Yellow-footed Honeyguide *Melignomon eisentrauti* (starting some seven hours after dawn). The daily duration of singing varies somewhat between species, the Yellow-footed having apparently the shortest (about two hours). Some species stop singing for 2–3 months each year (Lesser Honeyguide *Indicator minor*, Willcocks's), or for periods of several weeks (Lyre-tailed Honeyguide *Melichneutes robustus*, displaying mostly in the long dry season). Spotted Honeyguide may sing all year; we lack information for other species.

Site fidelity from one year to the next has been observed in several species. Within the same species regular song sites seem rather scattered (at least 1 km distant). The Lyre-tailed Honeyguide, however, may have a lekking system, with several individuals aerial-displaying in a restricted area; the special noise produced by this species appears to result from wing as well as tail movements. Almost nothing is known of the behaviour of Cassin's Honeybird *Prodotiscus insignis* (?aerial display), nor of the singing habits of Least Honeyguide *Indicator exilis*. Zenker's Honeyguide may behave rather like its congener, the Yellow-footed, with a limited singing period in early afternoon, but more information is necessary to complete the picture for this and other species.

The honeyguides (Indicatoridae) are an Old World family of Piciformes, with two species in Asia and 14 or 15 in Africa, depending on taxonomic treatment (Short & Horne 1988, 2001, Dowsett & Forbes-Watson 1993; see below). At least six African species, in the genera *Prodotiscus* and *Indicator*, are known to be brood parasites, and a seventh (Lyre-tailed Honeyguide *Melichneutes robustus*) is strongly suspected to be (Chapin 1939, Friedmann 1955, based on a nestling possibly taken from the nest of a barbet *Gymnobucco* sp.). All species eat insects, whilst those of the genera *Indicator* and *Melichneutes* are avid consumers of beeswax, and also (most *Indicator*) of bees and their larvae (Short & Horne 1988, 2001). The singing and breeding behaviour of four species is reasonably well known, due to field studies in eastern and especially southern Africa: these are Greater Honeyguide *Indicator indicator*, Lesser Honeyguide *I. minor* and Scaly-throated Honeyguide *I. variegatus* (Friedmann 1955), and Green-backed Honeybird *Prodotiscus zambesiae* (Vernon 1987).

The singing habits of the three *Indicator* species mentioned above were studied mainly by Ranger (1955) in South Africa, who was able to draw the following conclusions: males sing at traditional sites over many months each year; these sites are used by an individual, which, when it disappears, can be replaced by another male as soon as the next day; the same sites can be used for at least eight years and possibly up to 26 years in a Scaly-throated Honeyguide 'site', and at least 22 years in the other two species. In the case of Greater Honeyguide, a site consists of a series of trees in a particular area, some as far apart as 85 m; in the other two species, the site is usually more concentrated, especially in the forest-based Scaly-throated Honeyguide, which uses a tight cluster of a few trees. Ranger (1955) also remarked that Scaly-throated Honeyguide consistently sings in the understorey, whereas the other two use the canopy, and that the former species sings virtually year-round, whereas Lesser and Greater are more seasonal. There are also differences in the timing of singing during the day, Scaly-throated being especially early, starting from dawn, *c.*3 hours before the other two species. Vernon (1987) in Zimbabwe showed that Green-backed Honeybird sings in aerial displays.

Mating at or near the song site has been observed in the Greater Honeyguide (Friedmann 1955, Ranger 1955), and it is generally assumed that this is the purpose of song sites. Although Short & Horne (1988: 505) write that female Lesser Honeyguides come for breeding to the song site, actual mating was not observed by the authors cited in support (Friedmann 1955, Ranger 1955). However, by trapping in the immediate vicinity of the song site, Ranger and Skead (*in* Friedmann 1955: 189) found that at least six Lesser Honeyguides frequented the same spot. Later Short & Horne (2001: 458) wrote: 'Females . . . are attracted to the song sites, and sometimes may copulate there; most copulations occur away from song perches, usually in low trees or bushes'. Presumably this statement is based on their own unpublished observations.

Very little has been published on the singing habits of honeyguide species inhabiting the Guineo-Congolian rain forests (Friedmann 1955, Short & Horne 1988, 2001). This note presents information I have collected by opportunistic observations in the region, completed by what little has been documented in print, or through correspondence. It is hoped that this paper will encourage other observers to obtain and provide more information on the behaviour of this most intriguing group of birds. Most of my field observations are from northern Congo-Brazzaville and

Cameroon (1994–2001), and West Africa (Sierra Leone, 2007 and Ghana, 2004–05). Dawn was measured as first light when the first diurnal birds start singing (especially Chocolate-backed *Halcyon badia* and Blue-breasted Kingfishers *H. malimbica*). In Odzala National Park in northern Congo-Brazzaville, on the equator, dawn at different seasons varied from 05.30 to 05.50 hrs local time (GMT + 1). Sierra Leone to Ghana are included in the GMT time zone; of course dawn is earlier in Ghana (05.50–06.00 hrs in the forest zone, December–February) than in Sierra Leone (06.40–06.45 hrs in Gola Forest Reserve, January–February). Local time in Nigeria/Cameroon (GMT + 1) is fairly comparable to that in Côte d'Ivoire (GMT), as there is about one hour's difference in real time between the two countries.

Cassin's Honeybird *Prodotiscus insignis*. Guineo-Congolian near-endemic, found mostly from Sierra Leone (Short & Horne 2001) east to western Kenya (Zimmerman *et al.* 1996). This is an uncommon species of emergents or canopy in primary forest, or of secondary situations, degraded forest and farmbush with scattered trees (e.g. Brosset & Erard 1986; pers. obs.). The voice is poorly known and there are no tape-recordings (Chappuis 2000). Demey & Fishpool (1994) describe a 'distinctive buzzy *tsrrr-tsrrr-*. . . , uttered in flight'. This flight-song has been heard in several parts of its range (R. Demey *in litt.* 2007). By analogy with the other two species of *Prodotiscus* (Brown-backed Honeybird *P. regulus*, and Green-backed Honeybird) of savanna woodlands, one would expect this to form part of an aerial display. That of Green-backed Honeybird is well described by Vernon (1987): birds call in undulating flights 10–20 m above the canopy, giving a disyllabic, harsh *skeee-aa* (first described briefly by Benson & Benson 1948). This call is repeated several times at intervals of *c.*1 second. Displays persist for *c.*20 seconds and have been heard in all months, but with a clear peak in the breeding season (August–October in Zimbabwe). The aerial display of Brown-backed Honeybird, with spaced-out notes *tzit . . . tzit . . . tzit*, is frequently heard in Zambian woodlands (e.g. P. M. Leonard *in* Leonard & Peters 1998, 1999).

Zenker's Honeyguide *Melignomon zenkeri*. Guineo-Congolian endemic, of Lower Guinea, from Cameroon (Short & Horne 2001) to western Uganda (Carswell *et al.* 2005). Although R. J. Dowsett and I came across this species several times in northern Congo-Brazzaville, Cameroon (in the south-east: Dowsett-Lemaire & Dowsett 2000, and at Mt. Kupe), and in mainland Equatorial Guinea (Dowsett-Lemaire & Dowsett 1999), we never heard one singing. The song, a rhythmic series of pure high-pitched whistles, was known to me since 1993 through a tape-recording by T. Gullick, obtained on 25 September 1992 at Mt. Kupe. An earlier recording of a bird singing at the same site was obtained by R. Martins (21 October 1991) and published by Chappuis (2000). T. Gullick (*in litt.* 2007) noted that the bird was singing at mid levels ('20–30 feet up') below the canopy of a large tree, and this was at *c.*14.00–15.00 hrs. R. Martins (pers. comm. 2007) also tape-recorded the bird in the early afternoon. M. Andrews showed us the song post in March 1997: the site was a large *Aningeria altissima* on the edge of evergreen rain forest which had recently been logged by farmers for planks; the altitude was 1,050 m. On the morning of 1 April we saw a Zenker's Honeyguide in the area, flitting and flycatching in trees around the treefall. It was in moult (tail half-grown) and silent. On further visits to the area, in March–April, September and November 1998, the species was neither heard nor seen and it may be that the disappearance of the tree put an end to this song site. Bowden (2001) wrote that most singing was noted in September–October, but also through to April (in fact to March: C. Bowden *in litt.* 2007). He also mentioned a second song site at Mt. Kupe, without details: this was *c.*500 m distant, and possibly not a regularly used site (C. Bowden (*in litt.* 2007) heard a bird there on 27 February 1992, but did not visit regularly). C. Bowden (*in litt.* 2007) also noted that timing of calling was around midday to afternoon, and one calling period lasted *c.*2 hours. September–October coincides with the second half of the rainy season (the rains ending in November).

Yellow-footed Honeyguide *Melignomon eisentrauti*. Guineo-Congolian endemic, mostly Upper Guinea (Sierra Leone to western Cameroon: Short

& Horne 2001). The song of this species was tape-recorded for the first time by N. Borrow in Côte d'Ivoire on 31 December 2000, and described (with sonograms) by Rainey *et al.* (2003): each note of the series rises in pitch and the tone is somewhat reminiscent of a small raptor. Attracted by playback, the bird sang at a height of usually *c.*30 m, and the time of day was around 14.00 hrs (N. Borrow *in litt.* 2007). On 1 March 2002, R. Demey and L. D. C. Fishpool (*in* Rainey *et al.* 2003) heard the song in another forest in Côte d'Ivoire; it came from just below the canopy, at a height of *c.*15 m, and the time was *c.*13.00 hrs (L. D. C. Fishpool *in litt.* 2007). Both sites in Côte d'Ivoire were in semi-evergreen rain forest. A bird heard by L. D. C. Fishpool in Nigeria (Okomu National Park, 19 November 2004) was singing at *c.*14.30 hrs (L. D. C. Fishpool *in litt.* 2007). Another heard by R. Demey (*in litt.* 2008) in Liberia (North Lorma National Forest, 21 December 2005) sang once at *c.*13.00 hrs, at mid levels in moist evergreen forest.

Assisted by a copy of N. Borrow's tape, I identified the song of this honeyguide in the Atewa Range Forest Reserve, Ghana, on 6–7 February 2005. The forest at Atewa is upland evergreen rain forest (a little over 700 m). The bird was singing in dense vegetation over a stream at mid levels (15–20 m) near a small clearing; in the two days I spent in the area, it sang for a limited period, between 13.30–15.30 hrs (6 February) and 13.20–15.15 hrs (7 February), i.e. starting seven hours and 20/30 minutes after dawn. Song phrases were interrupted by pauses of up to several minutes. When a tape was played *c.*50 m from the tree, the bird went silent for five minutes before singing again. Playback was tried once more, closer to the tree: the bird went silent, located another bird in the same tree and gave chase, both birds flying out of sight. This was at 15.15 hrs and the bird did not sing again that day. On the morning of 7 February a Yellow-footed Honeyguide was seen flycatching in medium-sized trees within 100–200 m of the song post.

During a five-week survey of Gola Forest, an evergreen rain forest in Sierra Leone, in 2007, Yellow-footed Honeyguides were heard singing at two locations. The first was singing in dense vegetation at mid levels (*c.*25 m) in 40-m tall primary forest, on 5 February. It sang from at least 14.00 hrs (not yet by 13.00 hrs, when I first crossed the area) to 15.20 hrs. During that period, it paused twice, for 10 and 17 minutes respectively. The second bird was heard on 21 February, in similar forest, at 14.40 hrs to at least 15.12 hrs. Dawn was at 06.45 hrs, thus a bird singing from 14.00 hrs or slightly before would start about seven hours after dawn, much as in Ghana.

Only the bird in Atewa was heard for the full singing period, which lasted two hours on both days of observation. Overall the species has been heard singing in the months of December–March, in the main or only dry season. The song appears to carry several hundred metres.

Spotted Honeyguide *Indicator maculatus.* Guineo-Congolian near-endemic with a wide range, from The Gambia (Short & Horne 2001) east to western Uganda (Carswell *et al.* 2005). Although the species was not tape-recorded prior to the early 1990s (by C. Carter in Ghana, and myself in Congo-Brazzaville), its burring, rising trill was already well described by Williams (*in* Friedmann 1955) and is a characteristic sound of Guineo-Congolian forests; it is virtually identical to that of the extralimital Scaly-throated Honeyguide. It is possibly the commonest honeyguide of any genus in primary forests of the region, and is encountered in any evergreen as well as semi-evergreen rain forest types, primary to old secondary. In The Gambia it occurs in forest but also in degraded wooded savanna (N. Borrow *in litt.* 2007). In Cameroon it ascends into montane forest, to 2,100 m (a bird mist-netted by M. E. O'Kah pers. comm., on Mt. Manenguba), but I have not located a single song post in the Kupe/Bakossi/Manenguba area.

Spotted Honeyguide is very much a species of the understorey, and its presence in mixed-species flocks is usually detected by its 3–4 whistled *foui-foui-foui* calls, somewhat reminiscent of those of a scimitarbill *Phoeniculus* sp., and identical to those of Scaly-throated Honeyguide (pers. obs.). These calls can also be transcribed as '*peeeoo-peeeoo*' (Barlow *et al.* 1997) or '*woe-woe*' (Short & Horne 1988). The song is emitted from a shady position in dense understorey, at mid levels (*c.*10–15 m high in 30-m tall forest, but the position of several birds was not located precisely). From Congo-Brazzaville and Cameroon west to Sierra Leone I have come across 21 different singing birds, and all were heard in the morning, with one exception. The song is audible from a distance of at least 200–300 m. The main song period is overall from one to six hours after dawn, but singing possibly starts even earlier, as I rarely had the opportunity to check or reach a song site by dawn. In Gola one was not yet singing 30 minutes after dawn, but it was when I recrossed the area 40 minutes later; on another day it was singing from at least one hour after dawn. In Ghana (Atewa) one was singing intermittently in the afternoon, between 16.00 and 17.00 hrs (thus more than ten hours after dawn).

How many hours a particular individual sings each day has not been measured accurately, but is at least 3–4 hours, and possibly as many as five hours. In Congo-Brazzaville, one song post at Odzala was occupied for at least one year; another in Nouabalé-Ndoki National Park was relocated on a second visit in May, 13 months after the first. A site in The Gambia was occupied for at least two years (N. Borrow *in litt.* 2007). In northern Congo-Brazzaville and adjacent south-east Cameroon I have heard the song at all seasons, and in all months except June–July (when I was not in the field). Information from West Africa is less complete.

In most forest localities, only one song site was discovered; in Gola, where I found four, the distance between the two nearest was several km. It is surprising that in the mountains of western Cameroon, where this species was frequently recorded (mist-netted, or call-notes heard in mixed flocks), not a single song post could be found in March–April 1998, November–early December 1998, February 1999 and March 2000.

Lesser (Thick-billed) Honeyguide *Indicator minor* (the forest form *conirostris*). The form *conirostris*, treated as a separate species by some authors, is a Guineo-Congolian near-endemic which reaches western Kenya, but the precise range limits of this and the peripheral *I. minor* are unclear: the voice of the two forms is indistinguishable (Chappuis 2000) and plumage differences are slight, nominate *conirostris* having darker underparts than other races (Short & Horne 1988, Borrow & Demey 2001). However, the western race *ussheri* of '*I. conirostris*', which occurs in the Upper Guinea forests east to Ghana, is much paler below and could be a race of *I. minor* (Short & Horne 2001). Lesser Honeyguides *sensu lato* are widespread in the Guineo-Congolian region, inhabiting evergreen and semi-evergreen formations, primary and secondary, lowland and montane. In western Cameroon, singing birds were heard as high as 1,700 m (Mt. Manenguba, February 1999: pers. obs.), and there are records of silent birds up to 2,200 m (Mt. Oku, where a mist-netted bird was attributed to *conirostris*: Stuart 1986). In Liberia it has been heard to 1,550 m on Mt. Nimba (Gatter 1997).

I came across at least 32 different singing individuals, two of which were in study sites visited many times over a total of 13 months (in Odzala, Congo-Brazzaville). Birds sing just below the canopy in the foliage of tall trees, and can be very difficult to locate; one at Odzala sang from at least two or three neighbouring trees. Still at Odzala, the precise time an individual started singing was noted 15 times at different seasons: from 09.00 to 11.45 hrs, but most often between 10.00 and 10.35 hrs (n=11), i.e. from three hours and 10 minutes to five hours and 55 minutes after dawn, mean four hours and 40 minutes. The onset of singing could be quite variable at the same song site in the same month: e.g. the time noted on four different days in January 1994 varied from 10.25 to 11.45 hrs. It appeared that the bird tended to start later on an overcast day, and reasonably early (before 11.00 hrs) on a sunny day. The full duration of singing was noted only twice and was three hours (09.00–12.00 hrs, April) and three hours and 45 minutes (11.00–14.45 hrs, January), respectively. Excluded from these counts are two occasions when the bird was hardly singing at all, at the end and at the beginning of the singing season, on 12 September and 19 November. On those dates, it gave just a few songs in the middle of the day (11.30 hrs and 13.00 hrs respectively) and none at all between these dates (on several visits). Another bird checked monthly was singing on 6 September and 13 December but not on 12 October or 12 November.

Observations elsewhere in the Guineo-Congolian region largely concord with those from Odzala, i.e. showing the pattern of a late morning and midday singer: two birds, however, were singing in mid-afternoon (15.00–16.00 hrs) on the slopes of Mt. Manenguba, at 1,550 and 1,700 m, in February 1999. Possibly in cool environments singing could be displaced slightly later in the day. Of some 28 other individuals, the song was heard between 3–4 hours to 8–9 hours after dawn. One bird in Gola, starting at 09.00 hrs (February 2007), only two hours and 20 minutes after dawn, was exceptionally early; on another day at the same site, a bird was singing at 14.00 hrs but the starting time was not known—assuming it had started as early as 09.00 hrs, the duration of singing would have been at least five hours.

One of the Odzala birds was singing in the same location from January 1994 to March 1995 (with interruptions, as above), and the other site was occupied for at least one year. At Nouabalé-Ndoki one song post located in April 1996 was still occupied 13 months later on a second visit. In Yapo Forest, Côte d'Ivoire, Demey & Fishpool (1994) mention a song site high in the canopy occupied from May to January in three consecutive years.

On seasonality, the Odzala records show a clear interruption for a period of two months, from mid-September to mid-November, in the longer of the two rainy seasons. In Yapo, Demey & Fispool (1994) noticed an interruption of three months, from February to April (end of dry season, early rains). In Ghana, however, I heard them in all months of field work, from December to April (dry season to early rains) and in July–August (in the rains, Kyabobo). In Sierra Leone, the singing output of two different birds on 27 January and 20 February was so low—only a few phrases in the middle of the day—that it suggested these birds were only just starting again, after a period of vocal rest: by 22–25 February another individual was singing quite vigorously. In Cameroon generally, songs have been heard in all months from November to April (dry season, early rains), but I was not in the field at other seasons, except briefly in September.

Song sites are normally quite scattered: one exception to this was two birds singing within 150 m of each other, in secondary forest on the southern edge of Atewa (Ghana), in February 2005. As this area was visited for only one day, it is unknown whether both of these were 'traditional', well-established sites. In Gola, where three singing birds were located, the nearest two were *c.*5 km apart.

Least Honeyguide *Indicator exilis.* Guineo-Congolian near-endemic with a wide range throughout the forest region and extending into montane and transition zones, to western Kenya (Zimmerman *et al.* 1996) and north-western Zambia (Benson *et al.* 1971). Its song is almost a high-pitched version of that of Lesser Honeyguide (Chappuis 2000). Very little is known of its singing habits (Friedmann 1955, Short & Horne 1988). In Central and West African forests, it may be the rarest of all *Indicator* species: at Odzala and Nouabalé-Ndoki the few birds seen (one mist-netted) were associated with the edge of swamp forest, but I never located a singing bird. In Lobéké National Park, south-east Cameroon, one was singing in swamp forest at the edge of a large marsh, on 19 December 1997, around 10.00 hrs. In March 2007, N. Borrow (*in litt.* 2007) heard one at Mt. Kupe singing in secondary forest at *c.*16.00–17.00 hrs. In north-east Gabon, Brosset & Erard (1986) noted a peak in vocal activity during November to February (centred on the hot dry season). In montane forest of the Albertine Rift, I heard it only once in Nyungwe Forest, Rwanda, between late September and early February, on 25 November, when perhaps out of season (Dowsett-Lemaire 1990). Two were singing at 2,100 m in Bwindi Impenetrable National Park, Uganda, on 20 February 1990: these were within hearing of each other, but the exact distance was not noted. A bird tape-recorded in Guinea (Foulayah, 3 November 1991) was singing late morning in the canopy (R. Demey *in litt.* 2008).

Willcocks's Honeyguide *Indicator willcocksi.* A widespread Guineo-Congolian near-endemic, from Guinea-Bissau (Rodwell 1996) to Uganda (Carswell *et al.* 2005) and Rwanda (Dowsett 1993), extending locally into riparian forests of the Sudanian region, e.g. in southern Chad (Chappuis 2000) and northern Ghana (Mole National Park and Gbele Reserve: pers. obs. 2005). A fairly common species of evergreen and especially semi-evergreen rain forests, primary and secondary, and more locally in drier (in Gbele largely deciduous) riparian forests. The song, a rhythmic series of modulated whistles ending in a *wit* or *wik* note, is readily identified by this final note (Chappuis 2000). Pallid Honeyguide *I. meliphilus* of eastern Africa has a very similar whistled song, also ending in a *wit* (pers. obs. in Kenya; there are no commercial recordings, as the tape published by Chappuis (2000) from Zimbabwe is in fact of Lesser Honeyguide). These songs sound rather weak for honeyguides, but the position of the songsters (see below) permits them to be heard up to 100–200 m, and probably more at canopy level.

In 1994–2007, I came across 20 different song sites, six of them in Nouabalé-Ndoki, Congo-Brazzaville, where the open canopy of semi-evergreen rain forest seems particularly suitable. A remarkable feature of singing birds is their position: they occupy the tallest trees of the forest, usually emergents of great size, often *c.*50 m in height. Another, even more remarkable, feature is that they show a preference for certain tree species: of 16 'song trees' located and identified, nine were *Piptadeniastrum africanum*, a Mimosaceae with a broad flat crown and feather-like foliage. All six song sites in Nouabalé-Ndoki were in this tree, and others have been found in Odzala (one) and much further west in Gola, Sierra Leone (two). Another favoured tree is *Ceiba pentandra* (five cases): one in Odzala on the edge of a river, two in lowland Bakossi, Cameroon, in secondary forest, and two in Bia National Park and Atewa, Ghana. Other tree species used include *Albizia* sp. (one, in secondary forest south of Mt. Nlonako, Cameroon), and *Khaya senegalensis* (one, Mole, Ghana). The bird can often be very difficult to see, but sometimes was observed to change perches between song phrases, and also to preen or feed intermittently. *Piptadeniastrum*, *Albizia* and *Ceiba* have in common a broad crown and rather light foliage, permitting good visibility for any bird choosing a position in their crowns; they are also favoured by avian insectivores, attracting at times large mixed-species flocks. *Piptadeniastrum* is widespread in northern Congo and elsewhere, but it is not one of the commonest emergents (pers. obs., see Dowsett-Lemaire 1996 for Odzala), thus choosing a *Piptadeniastrum* so frequently cannot be dictated by chance.

Much like Spotted Honeyguide, this is a morning to midday singer, but it tends to start *c.*2 hours after dawn: thus a bird in Nouabalé-Ndoki and another in Gola both started exactly two hours after dawn, and continued singing for several hours until early afternoon. The Congo bird was followed for a full day and sang with short interruptions for seven hours, from 07.30 hrs to 14.30 hrs, with a few phrases again at 16.00 hrs! At 11.00 hrs, it moved to a neighbouring *Piptadeniastrum* and sang there for the rest of the day. That in Gola was heard partially over four days: it stopped singing on two different days by 14.00 and 15.10 hrs (thus seven hours and 15 minutes to eight hours and 25 minutes after dawn). The maximum duration of singing (starting and ending were noted on different days) would have been six hours and 20 minutes. Like the Congo bird, it once moved to a neighbouring *Piptadeniastrum* to sing, in the early afternoon.

All of the other 18 singing birds were encountered in the morning, from 2–3 hours after dawn until noon or early afternoon (up to eight hours and 30 minutes after dawn). One song site in Odzala was still occupied 14 months after I first found it; another in Nouabalé-Ndoki was still used in May 1997, 13 months after my first visit. One song site in Atewa used in February 2005—a *Ceiba* on the slope above the gate (pers. obs.)—was still used in August 2006 (A. Hester *in litt.* 2006).

On the seasonality of singing, data are few: one bird followed intermittently at Odzala from January 1994 to March 1995 was clearly silent in September–October; it was last heard in late August, and started again, briefly, on 22 November, in another tree. It had returned to its regular tree and sang more frequently from December. This is very similar to the period of silence observed by a Lesser Honeyguide in the same forest. Elsewhere, in Cameroon and Ghana, songs have been heard throughout the main dry season (late November to March) and beyond (including April, Cameroon, and August, Ghana). For Liberia, in addition to some of the dry season, Gatter (1997) has heard it in September.

As in other species, song sites appear to be rather scattered. At Nouabalé-Ndoki, the two nearest sites were *c.*1 km apart, but one of them was a 'new' site (in Bomassa camp, occupied in 1997, not 1996), and it is unknown whether this situation persisted. In lowland Bakossi, two sites were also *c.*1 km distant, whereas in Gola, the distance between two sites was *c.*3 km.

Lyre-tailed Honeyguide *Melichneutes robustus.* A Guineo-Congolian endemic, from Sierra Leone (Short & Horne 2001) to western Uganda (Carswell *et al.* 2005). Of limited distribution in West Africa, with definite records only from Sierra Leone to Côte d'Ivoire, but widespread in Liberia (Gatter 1997), it may also reach extreme southwest Ghana (Dowsett *et al.* in prep.). The species can be locally common in Central Africa. It occupies the higher strata of evergreen and semi-evergreen rain forest types, with a predilection for the vicinity of rivers, streams, or forest bordering swamps (Brosset & Erard 1986, Dowsett-Lemaire 1997a; pers. obs. elsewhere in Congo, Cameroon, Sierra Leone, and the observations of R. Demey (*in litt.* 2008) in West Africa). In western Cameroon I have heard its display up to 1,200 m, in the Bakossi and Nlonako Mountains. In Liberia Colston & Curry-Lindahl (1986) reported it up to 1,000 m on the slopes of Mt. Nimba.

This species has a remarkable aerial display, producing a series of 10–30 double nasal sounds, transcribed variously as '*nyêté, nyêté*, . . . ' (Chapin 1939), '*hein-hein-* . . . ' (Rougeot 1951), '*heyih heyih* . . . ' (Borrow & Demey 2001). The bird rises 100–200 m in the air and is extremely difficult to locate when the noise is actually produced, during the descent: the general display was well described by Rougeot (1951) from Gabon. In a later publication (1959), Rougeot specified that the noise seemed to be produced by the movements of both the tail and wings: 'j'ai pu noter aussi l'ouverture saccadée des ailes, chaque fois ramenées au corps, et l'ondulation des rectrices'. On another occasion, he saw that the bird 'entr'ouve les ailes par saccades, la queue aussi', later again 'lors de sa chute . . . , entr'ouvrant convulsivement et simultanément les ailes et les rectrices. A chaque mouvement semble correspondre l'étrange et double vibration.' In summary, each noise seems to be produced by the quick opening and closing of wings and tail. From a recent observation in Gabon by A. S. Riley and J. Rossouw (*in litt.* 2006), it appears that the wings indeed play an important role in the production of the noise: 'it appeared to us that the noise was produced by the wings, not the tail as it held its wings in an out position before each "call", whereas the tail was seen to splay only at the bottom end of the display long after the noise began'. Short & Horne's (1988, 2001) brief descriptions of the display mention only the role of the tail, thus not giving full justice to Rougeot's observations.

At Odzala, where the species is locally common, displays were heard at all seasons, but with short interruptions, of 1–3 weeks, at any time of year. However, a longer interruption of *c.*6 weeks was centred in March: in 1994, the last display was heard on 25 February and the first one again on 12 April; in 1995, the last was heard on 24 February and none had been heard again by the time I left, on 7 April. In north-east Gabon, Brosset & Erard (1986) found the species displayed most actively in the cool dry season (May–September), and more sporadically at other times. Rougeot's (1951, 1958) accounts are more detailed, suggesting that maximum activity is achieved in June–October (dry season and start of main rains); in some years it can be silent in late April–May, but noisy in other years (or localities). In 1957 there were no displays from 7 October to 27 November. In Liberia, Gatter (1997) heard them mainly in the dry months of November to April.

At Odzala most displays were performed 1–3 hours after dawn, and rarely in late afternoon, an hour before dusk. In Cameroon the pattern seemed similar, with most displays in the morning, rarely late afternoon. In Sierra Leone, in February 2007, displays were heard regularly over the Mogbai stream from one hour to two hours and 30 minutes after dawn. In cool, misty weather, displays can be given much later, in the middle of the day or early afternoon: thus in June 1989 in the Mayombe, Congo-Brazzaville (in the cold dry season), displays were heard sporadically from noon to 15.00 hrs. In the cool dry season of Gabon, Rougeot (1958) noted most displays at 08.00–11.00 hrs, and sometimes also in the afternoon.

Often displays are heard from different locations in a limited area, i.e. a few hundred metres from each other (as along the Mogbai, a forest stream in Gola), and it is impossible to ascertain how many individuals are involved. In June 1989 in the Mayombe, near Dimonika, they were heard at different points along 3 km (Dowsett-Lemaire & Dowsett 1989). At Odzala, as my boat was moving slowly down the Lékoli River (14 October 1994), I heard displays overhead every *c.*1 km over 4 km. In this case, it seems that at least four different individuals were involved. Brosset & Erard (1986) make similar comments on the distribution of displaying birds along the Ivindo River of Gabon, with inter-distances of *c.*1 km; in one area, in July, they found a concentration of 2–5 individuals displaying within 200–300 m of each other. Rougeot (1958) sometimes noted two individuals displaying close to each other. I agree with Brosset & Erard's (1986) suggestion that this system of local concentrations is indicative of lekking behaviour. In Liberia, Gatter (1997) noted 'up to two birds heard several times in one place'. In Gola I found one pocket of displaying birds in one area, along 1–2 km of the Mogbai stream, but none in other, apparently suitable, sections of the forest.

Discussion

Of the eight forest species considered here, information on Cassin's, Zenker's and Least Honeyguides is scanty, and the discussion deals mainly with the other five. Of the four better-known *Melignomon* and *Indicator* species, some interesting patterns to their singing behaviour are beginning to emerge.

1. There is apparently a vertical separation between species, from Spotted Honeyguide singing in the under- to midstorey and Yellow-footed in the midstorey, to Lesser in the canopy and Willcocks's in emergents. Their respective vertical situation may be to some extent related to the type and volume of noise produced. It is hard to imagine that the tiny voice of Willcocks's could be heard efficiently through a wall of dense understorey vegetation, whereas the penetrating purr of Spotted Honeyguide does persist over at least 200–300 m in such situations. Other factors may be involved, including specific feeding techniques: birds feed on insects between singing bouts, and their respective positions in the forest may be partially conditioned by their feeding niche. There is no doubt that Spotted Honeyguides not only sing but conduct much of their feeding in the understorey, and it is the most frequently mist-netted species overall. At Odzala, I captured altogether 13 Spotted Honeyguides for two Willcocks's and no Lesser, even though my main mist-netting area was adjacent to a song site of Lesser.

The predilection of Willcocks's for certain large tree species is most peculiar, and it would be interesting to establish whether the species' closest relative in eastern Africa, Pallid Honeyguide, possesses such preferences. In November 2006 I located a singing bird in a large Baobab *Adansonia digitata* emerging over coastal thicket in Kenya, its position being very comparable to that of a Willcocks's in a forest emergent. C. Jackson (*in litt.* 2007) knows two song sites of Pallid within and near Arabuko-Sokoke Forest, both in tall trees (one in a eucalypt, and the other in an emergent *Erythrina*).

2. Each species appears to adopt a particular timetable for singing. The earliest to start is Spotted (an hour after dawn, possibly even earlier), followed by Willcocks's, Lesser and Yellow-footed. Although the number of observations of Yellow-footed is still small, it nevertheless includes seven different individuals in five different countries, all showing the pattern of an early-afternoon singer: this is the latest of all species, starting only *c.*7.5 hours after dawn. Zenker's Honeyguides at Mt. Kupe were also noted as singing in early afternoon.This is important to bear in mind in surveys, as species singing late in the day may be more easily overlooked. Lesser Honeyguides in savanna environments are known to start singing *c.*3 hours after dawn (Ranger 1955), or slightly earlier (*c.*2 hours; pers. obs.). It appears that most individuals in forest regions start mainly about four hours after dawn, or even later: possibly this slight shift in time is due to different feeding conditions in a more shaded forest environment. This is suggested by the observation that a Lesser Honeyguide at the same site in Odzala started singing earlier on sunny than on dull days.

Concerning the duration of singing, my observations are based on rather few completely measured singing periods, but it seems that Yellow-footed Honeyguides (*c.*2 hours) do not sing for as long as Willcocks's (up to seven hours), and Lesser and Spotted may be somewhat intermediate. If further information confirms this tendency, the question arises as to how some species can spend so much time singing, as opposed to feeding, even if some feeding occurs at the song site. Could this be related to the amount of beeswax consumed, as opposed to the more time-consuming insectivorous activities? So far, and unlike the *Indicator* species, *Melignomon* honeyguides are not proven to raid hives to eat beeswax (Short & Horne 1988, 2001).

3. A few song sites are known to have been occupied for a year or more, by Spotted, Willcocks's and Lesser (up to three in the latter). One Zenker's Honeyguide at Mt. Kupe was singing at the same site in 1991, 1992 and 1993 (C. Bowden *in litt.* 2007); and it was still present in 1997. This matches Ranger's (1955) observations on site fidelity of honeyguides in South Africa, and C. Jackson (*in litt.* 2007) wrote that the eucalypt in Arabuko-Sokoke has been occupied by a Pallid Honeyguide for at least nine years (since 1998). There is, however, still a long way to go before we know as much as Ranger did about long-term occupancy and the relative position of different song sites.

4. Inter-site distances are difficult to measure, and in a dense forest environment a singing bird can be easily missed if slightly off-track. The general impression is that song sites appear to be widely scattered. The distances of *c.*1 km in the case of two Willcocks's (in Congo and western Cameroon) and 150 m for two Lesser Honeyguides are the shortest measured between two sites. In the latter this is probably unusual: one of the two could have been a 'satellite' site in the meaning of Ranger (1955), who demonstrated that one of two close sites in Scaly-throated Honeyguide (280 m distant) was not attended regularly and was eventually abandoned. In his Lesser Honeyguides, some 'satellite' sites 500–800 m distant were either abandoned, or instead became the main site after the 'old' one was abandoned.

Almost nothing is known concerning the proportion of the adult population singing birds represent. Catching and ringing as many individuals as possible could help, but of forest species only the Spotted Honeyguide would lend itself to such a study, as the other species are too infrequently mist-netted. In Odzala, only one song post of Spotted Honeyguide was located in a section of forest where 13 birds were ringed, and the species was also the most frequently observed honeyguide, especially around beehives. In the mountains of western Cameroon, call-notes of Spotted Honeyguides were often heard and some birds were mist-netted, but no song post was located. This is reminiscent of the situation on the Nyika Plateau, Malaŵi/Zambia, at 2,000–2,300 m, where Scaly-throated Honeyguides were occasionally seen or their call-notes heard, and were definitely breeding (with three neighbouring nests of Olive Woodpeckers *Dendropicos griseocephalus* parasitised), but I never found a song post within a radius of several km around my main study area (Dowsett-Lemaire 1983). These fragmentary observations suggest that singing birds probably represent only a very small proportion of the overall population.

5. In Lesser and Willcocks's Honeyguides, a 'silent' period of *c.*2 months was clearly apparent at one study site (Odzala), and these birds also sang much less at the end or at the start of the singing season. An off-season of three months was highlighted in Lesser Honeyguides in Yapo (Demey & Fishpool 1994). This is shorter than the 6–7-month off-season observed in more seasonal South Africa, for Lesser (and Greater) Honeyguides (Ranger 1955). In South Africa this off-season falls outside the breeding season, and one can assume a similar pattern for the Guineo-Congolian region. A silent Zenker's Honeyguide observed at a traditional site at Mt. Kupe in April was moulting. I have too few data on moulting seasons of honeyguides at Odzala (Dowsett-Lemaire 1997b) to comment further.

Possibly seasonality is less marked in Spotted Honeyguide, as in Scaly-throated (Ranger 1955), but in general more information is needed on the question of seasonality for these and other species. That Lesser Honeyguides had stopped singing at Yapo in February–April (Demey & Fishpool 1994), at a time of year when (in 2005; pers. obs.) they were singing in neighbouring Ghana also poses further questions: can the season vary so drastically over a relatively short distance, or over different years?

Lyre-tailed Honeyguides possess a unique aerial display, given with varying intensity at different seasons, with a peak in the long or cool dry season.

Unlike perched honeyguides, they seem to be rather concentrated, in small pockets of a few displaying individuals (Brosset & Erard 1986; pers. obs.). However, more information is needed to confirm this.

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Appendix. Gazetteer of localities cited.
Annexe. Coordonnées des localités citées.

Arabuko-Sokoke Forest, Kenya	03°20'S	39°55'E
Atewa Range Forest Reserve, Ghana	06°10'N	00°35'W
Bakossi Mountains, Cameroon	05°00'N	09°40'E
Bia N.P., Ghana	06°35'N	03°05'W
Bwindi Impenetrable N.P., Uganda	01°03'S	29°40'E
Foulayah, Guinea	10°02'N	12°53'W
Gbele Reserve, Ghana	10°30'N	02°10'W
Gola Forest Reserve, Sierra Leone	07°30'N	11°00'W
Mt. Kupe, Cameroon	04°48'N	09°40'E
Kyabobo, Ghana	08°29'N	00°35'W
Lobéké N.P., Cameroon	02°15'N	15°45'E
Mt. Manenguba, Cameroon	05°00'N	09°50'E
Mayombe (Dimonika area), Congo-Brazzaville	04°12'S	12°22'E
Mole N.P., Ghana	09°30'N	01°50'W
Mt. Nimba, Liberia	07°32'N	08°32'W
Mt. Nlonako, Cameroon	04°50'N	10°05'E
North Lorma National Forest, Liberia	08°01'N	09°44'W
Nouabalé-Ndoki N.P., Congo-Brazzaville	02°20'N	16°30'E
Nyungwe Forest, Rwanda	02°30'S	29°15'E
Odzala N.P., Congo-Brazzaville	00°30'N	14°45'E
Okomu National Park, Nigeria	06°25'N	05°30'E
Mt. Oku, Cameroon	06°10'N	10°30'E
Yapo Forest, Côte d'Ivoire	05°42'N	04°06'W

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